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干旱区气候因子对枯落物分解和土壤动物的影响

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摘 要： 以土壤动物为主的碎屑食物网是枯落物分解及养分释放的重要途径，也是维持干旱-半干旱区脆弱生态系统生物地球化学循环和稳定性的关键环节。目前，土壤动物对枯落物分解的影响机制研究已成为当前研究的热点，但土壤动物与枯落物分解如何响应气候变化缺乏系统总结。从气候变化对枯落物分解的影响、气候变化对土壤动物营养结构的影响和气候变化对枯落物分解和土壤动物关系的影响3个方面，阐明气候变化通过改变水热因子和枯落物质量来影响枯落物分解功能和土壤动物的影响规律。现阶段对枯落物中土壤动物的研究仍停留在群落水平，而关于枯落物中土壤动物的营养结构和功能性状分布特征，尚未可知。因此，未来研究中，应注重大尺度、长时间的野外观测与控制试验相结合的方法，而且在机理方面需注重土壤动物功能性状对枯落物分解作用的研究。

关键词： 干旱-半干旱区；气候变化；枯落物分解；土壤动物

枯落物是陆地生态系统养分元素的重要载体，而且是连接地上-地下生态系统物质循环与能量流动的重要生态界面[1]。枯落物分解过程作为生态系统养分循环和能量流动的关键环节，其分解速率的细微改变能显著影响土壤碳收支、土壤肥力及陆地-大气碳交换[2]。土壤动物担负着消费者和分解者双重角色，是影响枯落物分解的重要生物因素，其群落多样性及生态功能显著影响着生态系统的生物地球化学循环和能量流动过程[3-5]。但对枯落物分解的贡献仍然是未知，且易被低估。土壤动物通过破碎、掘穴、取食、改变土壤性状和刺激微生物活动等作用，直接或间接的影响枯落物分解过程[6]。

全球干旱-半干旱区的面积约占陆地总面积的45%，生态环境脆弱，受气候变化的影响，旱区面积逐渐扩大。由气候变化引起的水热因子作为干旱-半干旱地区重要的调控因子，将深刻影响干旱区生态系统物质循环和能量流动过程[6-7]。枯落物分解是干旱-半干旱区土壤有机碳的主要来源，约占土壤有机碳的32%[7]。枯落物分解过程对水热因子响应变化将直接影响到干旱区脆弱生态系统的稳定[7-8]。同时，土壤动物是陆地生态系统中种类最为丰富的物种之一，其多样性远超于植被多样性[8]。在枯落物-土壤界面中，土壤动物食物网关系复杂，不同类群间联系紧密，一个关键种的丧失或群落组分的改变将会影响枯落物养分释放过程[9-14]。干旱-半干旱区的水热条件恶劣，土壤动物对枯落物分解的影响存在复杂性和特殊性，使得本区域的研究结果存在较大不确定性[13]。因此，综合分析气候变化背景下干旱-半干旱区枯落物分解与土壤动物的相关关系，掌握特殊生境下枯落物分解规律，对于维持该区域生态系统元素平衡，揭示土壤动物影响枯落物分解的潜在机理有重要意义。

1 气候变化对干旱-半干旱区枯落物分解的影响

1.1 温度升高对枯落物分解的影响

温度是调控生物地球化学循环过程的重要因子，同时也是影响枯落物分解的主要因素[14]。温度升高将直接作用于生态系统中水热条件，改变土壤质量、枯落物淋溶速率和微生物酶活性，影响枯落物分解过程[2]。

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国内外研究预测，到21世纪末期，全球地表温度将升高1.1~6.4 ℃，干旱-半干旱区的陆地覆盖面积将增加11%~23%，预示着枯落物的分解过程将处于增温状态中(表1)[12,15]。在室内控制试验中，温度升高可能通过提升土壤氮有效性和微生物活性来促进枯落物分解，且在40 ℃最大限度的促进枯落物中微生物的激发效应，加速陆地-大气碳交换[16]。而在长期控制试验中，温度升高2 ℃可以通过改变干旱区土壤-生物微生境来影响枯落物的分解过程。温度升高导致藻类结皮退化，促进了土壤与枯落物的混合，加速了枯落物的分解。而温度升高导致枯落物含水量降低，抑制了枯落物的分解速率，抵消了温度对枯落物分解的积极作用[17-18]。在海拔梯度代替气候变化试验中，温度作为高纬度旱区土壤生物活动和酶活性反应的重要驱动因子，温度升高加快其枯落物的分解过程[18-19]。在室内及野外试验中表明，温度升高将对干旱-半干旱区枯落物分解产生影响，但其响应模式因地域生境而异。

1.2 降雨变化对枯落物分解的影响

水分是影响干旱-半干旱区植被生长发育最主要的限制因子，是驱动生态系统物质循环和能量流动的重要因素，也是调控枯落物分解的重要因子[20-22]。首先，降雨促进枯落物中可溶性物质的淋溶，加速了枯落物的分解速率[23]。其次，降雨及冰雪冻融导致土壤干湿交替，加剧了枯落物的物理破碎，增加了土壤生物的数量和活性，有利于枯落物养分元素的快速释放[24-26]。

气候变化导致全球降雨格局改变，且地域差异显著(表1)[27]。在水分控制试验中，水分变化显著改变枯落物分解过程，干旱处理能够显著降低枯落物氮、磷养分元素的释放速率，并在降雨减少50%的处理中达到最高，分别降低了50.3%和2.7%[28-29]。在跨尺度降雨梯度试验中发现，实际蒸散与枯落物分解呈指数关系，是枯落物分解速率的有效预测因子[30]。研究表明，水分是干旱-半干旱区枯落物分解的主要限制因子，而干旱度升高将会严重影响干旱-半干旱区生态系统的能量流动与物质循环过程[28]。

近年来在降雨变化的同时，降雨极端事件也逐渐增多[27]。降雨事件多发生于植被生长季，呈降雨强度大且持续时间短等特点，属于脉冲式降雨[30-31]。降雨对干旱-半干旱区枯落物分解率的影响存在明显的季节变化。生长季期间，枯落物分解速率在降雨事件发生后迅速出现波动峰值[32]。降雨量控制枯落物中水溶性物质含量，直接影响枯落物分解过程；其次，降雨后枯落物干湿交替，促进枯落物微生物及土壤酶活性，导致枯落物分解速率波动变化[33-34]。而在非生长季期间，冻融现象使枯落物

表1 气候变化对干旱-半干旱区枯落物分解的影响

Tab. 1 The effect of climate change on the litter decomposition in semi-arid and arid ecosystems

研究样地	年均温/℃	年降雨量/mm	气候带	研究方法	研究结果
科尔沁沙地	6.0	343	半干旱区	增温：灯光加热	枯落物CO_2释放速率与温度呈显著正相关且在40 ℃时，枯落物CO_2释放速率达到最高[16]
毛乌素沙地	8.3	292	半干旱区	增温：开顶箱模拟增温	增温可能缓解干旱-半干旱区植物枯落物分解，并且温度对枯落物分解的抑制作用与分解时间和枯落物类型有关[18]
锡林郭勒草原	4.0	295	半干旱区	增温：海拔梯度代替气候变化	温度升高2.7 ℃，羊草和大针茅枯落物分解率提高35.83%和6.68%[19]
科罗拉多高原	14.4	241	半干旱区	增温：红外线灯光加热	温度升高2 ℃没有显著改变凋落物质量损失率，但环境变化影响了枯落物分解过程[17]
科尔沁沙地	6.0	343	半干旱区	降雨：自然降雨，减雨30%，减雨50%	降雨减少枯落物分解率和氮磷的归还[28]
古尔班通古特沙漠	4.0	150	干旱区	降雨：自然降雨，冬春增雪，夏季增雨	季节性短暂降雨增加对荒漠区枯落物分解无显著影响[21]
纳米布沙漠	10.0	75	干旱区	降雨：降雨季节变化	在干旱期，枯落物质量损失率为0%~16.7%；在湿润期，枯落物质量损失率为64.7%~97.2%。降雨是纳米布沙漠枯落物分解的最主要因素[34]
内蒙古荒漠草原	3.4	280	半干旱区	降雨：自然降雨，减雨30%，增雨30%	增减雨将显著改变植被根系的分解速率，首先影响根系的基质质量，进而影响根系质量残留率[24]

破碎化，加速枯落物中纤维素的降解，频繁的土壤冻融作用和冰雪融水淋溶作用显著促进枯落物在生长季初期的分解[24-26]。

1.3 光辐射对枯落物分解的影响

在干旱-半干旱区，植被覆盖度低，到达地表辐射量大，枯落物长期处于强光曝晒的环境下，光辐射深刻影响着枯落物的分解过程[35]。其中，光辐射增强引起的光化学降解通过氧化有机化合物，改变枯落物的理化性质，促进其物理淋溶过程[2,35]。在无菌条件下光照控制试验中，无光条件下枯落物分解率仅达15%，而光照条件下枯落物分解速率提升到35%~40%，表明在干旱-半干旱地区，光辐射引起的光降解是影响枯落物分解重要的非生物因素[36]。使用光波滤膜控制光源的枯落物分解试验中，发现紫外线和可见光均能够导致枯落物光降解过程，在光降解枯落物产生的总CO_2中紫外辐射和可见光分别贡献了55%和45%[37]。

随着全球臭氧层的减少，太阳紫外辐射尤其是紫外线-B将显著增强，且紫外线-B辐射的趋势至少持续到2050年[36]。为应对全球环境变化，在不同强度紫外线-B的枯落物分解试验中表明，紫外线-B辐射增加33%，拂子茅（*Calamagrostis epigeios*）枯落物分解速率将提升5%~10%[38]。在紫外光遮除试验中，紫外线-B引起的光降解解释了梭梭（*Haloxylon ammodendron*）、芦苇（*Phragmites australis*）和麦秆30%~85%的变异，且光降解对枯落物分解的贡献随降雨量变化一致，干旱区光降解促进枯落物分解，加速枯落物的淋溶过程[38]。同时，在季节性紫外线-B遮除试验中表明，旱季紫外线辐射是促进了下一个湿季枯落物的分解速率，表明干旱区枯落物中光降解作用受环境因子调控[38]。

2 气候变化对干旱-半干旱区土壤动物营养结构的影响

2.1 温度升高对土壤动物营养结构的影响

土壤动物对环境变化极为敏感，土壤温度的细微变化将显著影响土壤动物群落组成、多样性和营养结构特征[11]。在半干旱温带草原生态系统中，温度升高影响土壤动物的生活史过程，降低了土壤螨类和跳虫的丰富度[39-40]。在南非12 a野外增温试验中同样发现，温度升高导致草地中土壤动物丰富度下降37%[41]。这是由于土壤动物需在繁殖前经历寒冷期，温度升高将破坏土壤动物休眠期，致使土壤动物冬眠存活率降低，影响土壤动物的种群密度和丰富度[42-43]。

土壤动物类群的生态学特征差异，对温度阈值和敏感度不同，体型小的土壤动物具备发育繁殖快和生存活动小的特征，对温度变化更为敏感[11]。在内蒙古荒漠草原生态系统增温试验中，弹尾目、前气门亚目和螨类的密度和类群数在增温处理下降低，而中气门亚目在增温处理下升高[44]。温度升高对土壤动物食物网的影响表现为“热级联”效应改变“捕食者/猎物”比率，放大捕食效应，加强捕食者的“下行效应”，进而改变食物网结构[11]。地面节肢动物蜘蛛和甲虫等活跃在枯落物-土壤界面，温度升高增加了捕食者对螨类和跳虫的捕食作用[45]。在干旱-半干旱地区，土壤动物数量少且多样性低，捕食类群的细微变化都将导致营养联级效应，温度升高将显著改变土壤动物群落组成及多样性分布。

2.2 降雨变化对土壤动物营养结构的影响

绝大多数土壤动物生存在土壤孔隙中，其生命活动和生活史过程均依赖于土壤或枯落物水分，全球降雨格局变化将显著改变土壤动物群落分布[46]。尤其在干旱-半干旱地区，降雨变化将影响植被活性、土壤呼吸和初级生产力，直接或间接的影响植被-土壤动物群落组成和食物网结构，进而对生态系统结构和功能产生重要影响[47-48]。室内土壤湿度控制试验发现，湿度增加可促进弹尾目的取食和生长等代谢活动，显著增大弹尾目体长和生物量[49-52]。在美国沙地降雨控制试验中发现，线虫对降雨变化及其敏感，降雨能够显著提升线虫个体数，且食菌性线虫对降雨变化更为敏感[53]。而在科罗拉多荒漠研究发现，增雨能够显著改变变形虫类群数，但对土壤线虫和小型节肢动物的影响较小[54]。在干旱-半干旱地区，土壤动物与降雨变化密切相关，且反映出土壤动物对降雨的积极响应[54]。

随着气候变暖，极端降雨事件增多，降雨发生时间、持续时间和降雨量也将对土壤动物群落特征产生显著影响[55-57]。在Chihuahuan荒漠极端降雨脉冲试验中发现，极端降雨显著提高植食性线虫种群密度[58]。同时，在内蒙古半干旱气候区，土壤动物与降雨处理密切相关，与降雨量成线性关系[59]。极端降雨脉冲不仅改变中小型土壤动物生活史过程，

且对大型土壤动物的取食、生存和繁殖有显著的调控作用。在黑河中游干旱荒漠和宁夏荒漠草原生态系统中，土壤动物虫卵适宜在干旱的环境中孵化，而春季降雨脉冲降低了土壤动物孵化的成活率，直接影响了土壤动物的个体数分布。而夏季降雨将影响迁移能力强的大型土壤动物对栖息地的选择[48,60-62]。研究结果表明干旱-半干旱地区的降雨及极端降雨事件均会对土壤动物群落产生深刻影响，但不同土壤动物类群对降雨变化的响应各不相同。

3 水热因子对枯落物分解与土壤动物关系的影响

气候变化通过改变枯落物质量、枯落物分解过程和土壤动物群落，调控土壤动物对枯落物分解的影响[63]。(1) 水热因子将改变干旱区地上植被的种类，影响生态系统的演替过程，不同植被群落的枯落物含量及质量存在明显差异[64-65]。(2) 水热因子将改变土壤动物群落部分格局，显著改变土壤动物的群落组成和多样性分布[66-67]。在全球枯落物无脊椎动物分解研究计划中，土壤动物对枯落物分解速率的影响明显具有气候依赖性，土壤动物显著提高了温带气候区枯落物的分解速率。同时，枯落物分解速率与水热因子间拟合受土壤动物群落显著影响[68]。

气候变化导致植被类群由草本类植被向灌木转变，枯落物硬度、形态等物理特征可通过影响土壤动物的取食以及微生物的生存和繁殖显著改变枯落物分解过程[69-71]。同时，中小型土壤动物对枯落物的取食具有专一性，气候导致枯落物质量改变，通过影响土壤动物的选择性取食对枯落物分解产生深刻影响[72]。在枯落物界面，气候导致枯落物N含量升高可显著提高倍足纲马陆的生物量[73]。土壤动物在C:N(54.8)的枯落物中贡献率达41.5%，而在C:N(<32)的枯落物中贡献率仅19.52%[74]。枯落物的C:N含量限制了土壤动物对枯落物的摄入，影响马陆和木虱种群的繁殖能力[75]。在枯落物分解过程中，养分元素流失以及枯落物质量的改变，导致土壤动物群落特征表现出显著差异[76]。枯落物为土壤动物提供栖息地和食物资源，枯落物质量的改变直接影响土壤动物的生活史策略，通过其“自下而上”的调控对食物网结构造成深刻的影响[35]。整体而言，气候变化导致植被及枯落物的永久改变，必将对土壤动物造成长期影响，且具有时效性[72,77]。

气候变化直接作用于土壤动物丰富度、群落组成以及多样性，土壤动物对枯落物的贡献产生深刻影响[11]。在国内外跨尺度枯落物分解速率试验中发现，枯落物在其生长栖息地(主场)的分解速率要比在其他生境分解更快，提出了“主场效应”对枯落物分解的贡献可能比水热因子更高[78-79]。土壤生物对枯落物分解的特定作用被认为是枯落物分解“主场效应”的根本原因。其中，螨类尤其是甲螨亚目具有明显的生境特殊性，且中小型节肢动物迁移能力弱，往往具有很强的生境特化能力[80]。气候变暖致使美国Tennessee的中小型节肢动物群落结构改变，显著影响澳大利亚干谷线虫的物种组成及密度[81]。在德国Bremen 20 a的连续试验发现，气候变暖显著影响了跳虫群落的演替动态[72]。以上研究表明，气候变暖将显著改变土壤动物的群落组成及丰富度，食物网中关键种的丧失及群落组成的改变都将严重影响枯落物分解过程。

4 结 论

综上所述，气候变暖通过水热因子和植被群落的变化对土壤动物以及枯落物分解过程产生显著影响，但气候环境对土壤动物和枯落物分解间的相互关系不够明确。土壤动物对枯落物分解的贡献仍然是未知，且易被低估。枯落物作为碎屑食物链的起点和土壤动物的栖息地，对土壤动物的研究局限在群落水平，土壤动物群落的营养结构尚未可知，极大的限制了对土壤动物个体发育、种群变化和群落演替的认识。其次，气候变化导致水热因子的改变正不断改变枯落物质量及土壤动物群落结构，但还未有充足的证据证明，气候变化如何影响土壤动物群落，以及土壤动物群落及营养结构变化对干旱区脆弱的生态系统物质循环和能量流动过程产生的影响。

因此，未来应加强不同地域间团队合作，设计大尺度、长期试验，并结合严密的控制试验来开展相关试验研究。另外，针对土壤动物营养结构和种群水平分布特征，开展气候变化下土壤动物与枯落物分解间的研究来加强对土壤动物分解功能的解

释，更有助于理解干旱-半干旱脆弱生态系统稳定性和结构与功能的维持，为干旱-半干旱生态系统恢复、可持续利用及生态服务功能提供理论依据。

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Effects of climatic factors on litter decomposition and soil fauna in arid regions

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Abstract: Detritus food webs dominated by soil fauna were the main method of litter decomposition and nutrient release, which plays a crucial role in maintaining the biogeochemical cycle and stability of fragile ecosystems. It was an interesting topic regarding the research on the effect of climate change on litter decomposition in arid and semi-arid regions. Climate change may have an important impact on litter decomposition, soil fauna, and related factors. However, there is no systematic summary of the underling mechanism. This review based on relevant literature at home and abroad, summarizes the impact of climate change (temperature, precipitation, and solar radiation) on litter decomposition, the impact of climate change (temperature and precipitation) on soil fauna, and impact of climate change on the relationship between litter decomposition and soil fauna. It was suggested that climate change affects the correlation between litter decomposition and soil fauna regarding changes in environmental factors and litter quality. We proposed that the following prospects should be paid more attention in the future: (1) large-scale and long-term research, as well as strict control experimental setup; (2) functional traits of soil fauna; (3) ecological functioning of soil fauna on litter decomposition. It is suggested that the litter and soil fauna ecological research should give more attention to the interaction of environmental factors under climate change, the variations of litter decomposition at different spatial scales, and model establishment.

Keywords: arid and semi-arid regions; climate change; litter decomposition; soil fauna